The Life Cycle of *Cylindroiulus latestriatus* (Curtis, 1845)

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ABSTRACT

A population of *Cylindroiulus latestriatus* from Eastern Germany has been studied in 1983. On the basis of the characterization of stadia, by the defence gland method, all possible variations of increments of ring numbers are given and a scheme of developmental pathways is built up. By examining individual development and the resulting main pathways a review of the regularities in the development of ring increment in the species *C. latestriatus* can be made. The increment of body rings together with the increase of body length, volume, and biomass allows to clarify the regulatory mechanisms in the development of julids. The age structure and life cycle of the East German population of *C. latestriatus* is compared with those of other authors, made in different countries and habitats, and with different methods of stadial determination. They are generally in agreement with only minor differences.

RÉSUMÉ

Le cycle de vie de *Cylindroiulus latestriatus* (Curtis, 1845).

Le cycle de vie d'une population de *Cylindroiulus latestriatus* d'Allemagne orientale a été étudiée selon la méthode de comptage des glandes répugnatoires et comparée aux résultats obtenus par d'autres auteurs. Les divers modes d'acquisition de nouveaux anneaux sont explorés et l'hypothèse d'un mécanisme régulateur de l'ontogenèse des julides est testée sur le matériel étudié.

INTRODUCTION

The study of the post-embryonic development and the laws of anamorphosis in millipedes has a high level of interest. Life histories offer phylogenetical information and help to clarify relationships between millepede orders.

Despite there being more problems to overcome than in other groups (e.g. Chordeumatida, Polydesmida) the order Julida is, with 41 species investigated for developmental pathways, one of the most frequently studied orders. Difficulties in investigations arise from the overlap of ring numbers of successive stadia. The total number of rings cannot be used to determine the stadia. Maturity is reached in several different stadia and ages (see ENGHOFF, DOHLE & BLOWER, 1993). For this reason many more investigations on the life cycles of this order are necessary.

The species *C. latestriatus* has been studied very intensively by BLOWER & GABBUTT (1964) and by BIERNAUX (1972). Other authors (COTTON & MILLER, 1974; LANG, 1954) have given additional remarks to the life history of this species. No detailed investigations were known from Germany.

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This situation offers the rare possibility of comparing the results from different sites and by various methods of stadial determination.

MATERIAL AND METHOD

About 100 specimens of *C. latestriatus* were collected from the litter layer under hazelnut bushes in a garden at a very dry site in NE Germany (Premnitz near Brandenburg) in 1983. A more detailed description of the habitat is given by VOIGTLÄNDER (1987).

Irrespective of stadia and age, the specimens were reared at room temperature in Petri dishes with a natural substrate on a layer of moist filter paper to study the further development.

To identify the stadia of the freshly collected specimens I used the defence gland method (HALKKA, 1958; BROOKES, 1963). Measurements of length and width as well as weighing were made on living specimens (for the methods see VOIGTLÄNDER, 1987).

CHARACTERIZATION OF STADIA AND DEVELOPMENTAL PATHWAYS

The Table 1 shows the total numbers and increments of defence glands related to each moult. The first and by far the biggest variation in increase of rings (or defence glands respectively) occurs at the moult into the fourth stadium. From this there follows a nearly regular decrease both in variation and in newly occuring ring numbers.

TABLE 1. — Total number and increment of defence glands in *C. latestriatus*.

	n	n	increment of defence glands							
stadium	individuals	defence glands	8	7	6	5	4	3	2	1
II	33	1								
↓						100.0				
III	31	6								
↓			6.4	3.2	12.9	51.6	25.8			
IV	30	10-14								
↓				3.3	46.7	43.3	6.7			
V	42	15-19								
↓					40.5	42.9	16.7			
VI	45	19-25								
↓					4.4	66.7	24.4	6.7		
VII	45	24-29								
↓						4.4	28.9	66.7		
VIII	50	28-32								
↓								10.0	88.0	2.0
IX	29	31-34								
↓								6.9	65.5	27.6
X	16	32-36								
↓									12.5	87.5
XI	9	33-38								
↓										100.0
XII	5	34-39								
↓										100.0
XIII	1	38-40								
↓										100.0
XIV	1	40								

On the average, the highest increase in rings is gained during the moult into the Vth stadium. The following moultings show progressively fewer numbers of added rings, down to 1.0 from the XIth stadium on.

The pathways of defence gland increments (Fig. 1) are originally determined by the "basic groups", according to PEITSALMI (1981), occuring at the IVth stadium. Basic groups with the highest and lowest gland numbers become "normalized" during the following 3 moults.

Regarding the number of observed moulting events (indicated by the little numbers in Fig. 1), it is clearly visible that 2 or 3 main pathways of development (thick lines) dominate.

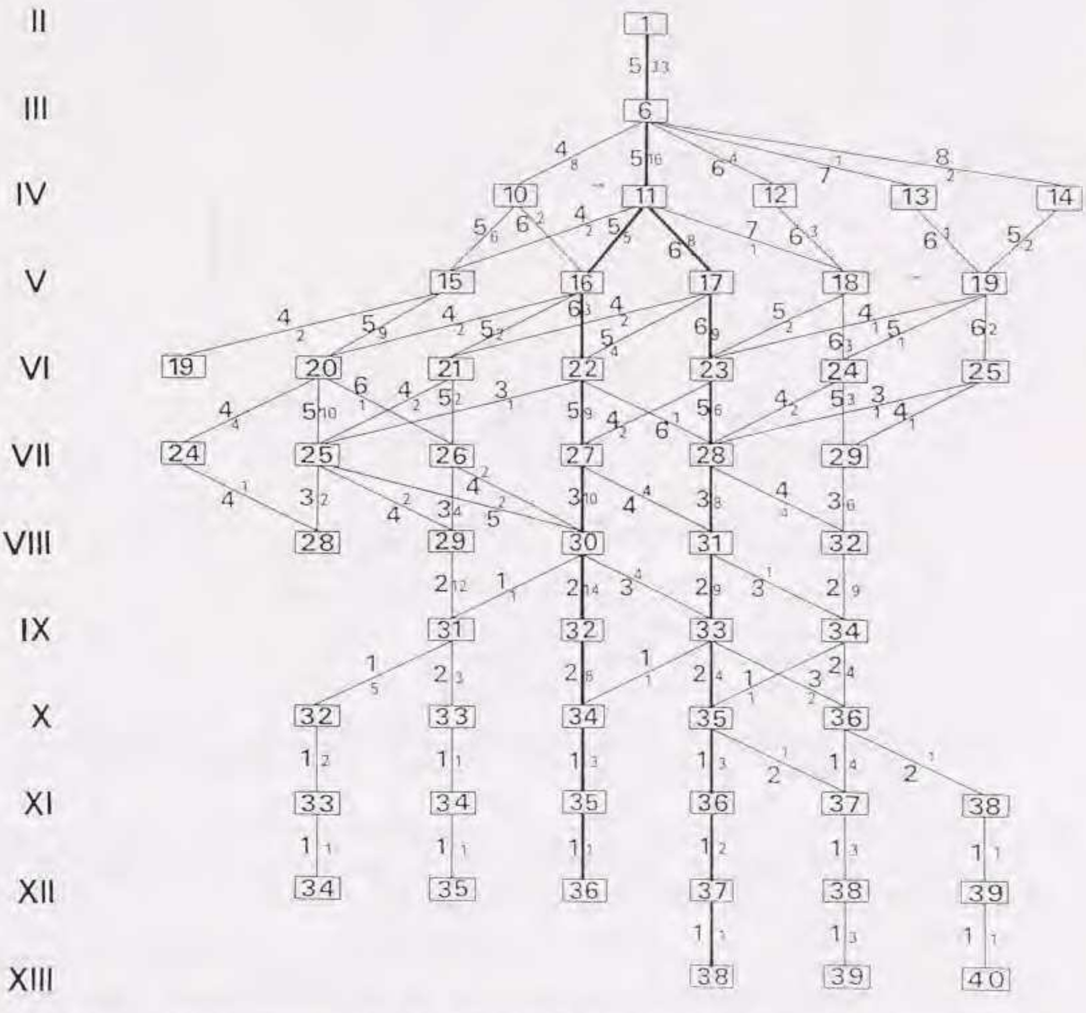

FIG. 1. — Observed defence glands and the main developmental pathways of *C. latestriatus*.

In Figure 2 the post-embryonic development of *C. latestriatus* is shown as a result of studies in an oak wood on sandy soil in England (BLOWER & GABUTT, 1964), in marram dunes on the east coast of Scotland (COTTON & MILLER, 1974), in a field of carrots in Belgium (BIERNAUX, 1972) and in a garden on sandy soil in Germany (this paper). The methods used for estimations were the analysis of discontinuities of dimensions (BLOWER & GABBUTT, 1964), the observation of eye rows (COTTON & MILLER, 1974; BIERNAUX, 1972) and the number of defence gland (BIERNAUX, 1972 and this paper).

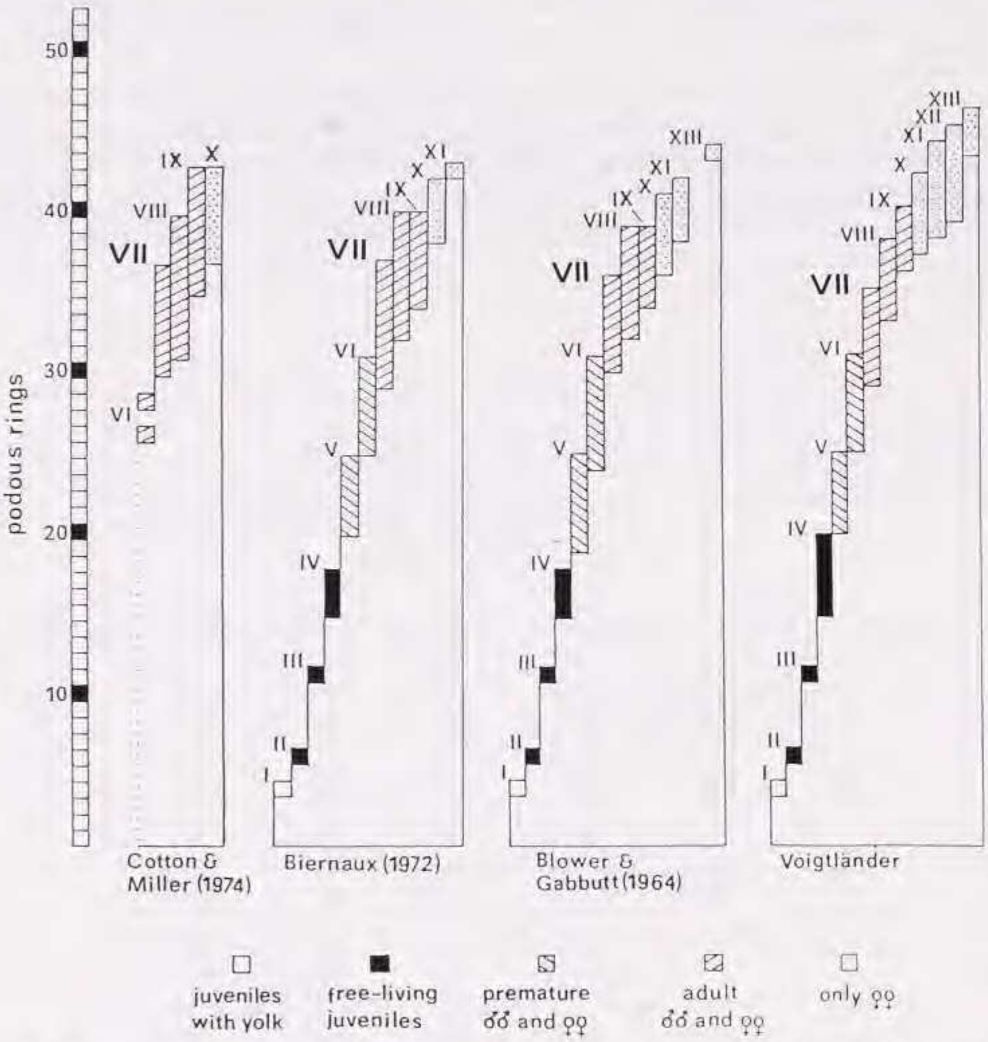

FIG. 2. — The post-embryonic development in *C. latestriatus* studied by different authors. The first stadium to contain mature animals is the stadium VII. Results by VOIGTLÄNDER deal with this paper.

Up to stadium IV there are few differences between the results. Later on variations increase, for example specimens of stadium XI show a maximum of 41 rings according to BLOWER & GABBUTT (1964), 42 rings according to BIERNAUX (1972) and 43 rings after the results of the present study.

Males reach stadium IX only, irrespective of the indicated ring numbers according to all authors. The highest stadium reached by females is stadium XIII, showing 43 rings (BLOWER & GABBUTT, 1964) or 45 rings (this work). COTTON & MILLER (1974) estimate the highest stadium being X with up to 42 podous rings. They argue that some females which were placed in stadia IX and X in their investigation may belong to stadia XI or XII because it is difficult to determine the addition of ocelli to the ocular field at higher stadia.

The results of the investigations of stadial development of *C. latestriatus* correspond with the rules known for other Juliformia. The species belongs to the group of anamorphotic julids with an indefinite number of body ring increments.

As in other related species, such as *Cylindroiulus punctatus* or *Kryphioiulus occultus*, older stadia add one new body ring only at each moulting.

C. latestriatus reaches stadium XIII as a maximum. The low number of stadia seems to be typical for Cylindroiulinae (for example *Enantiulus nanus* XV, *K. occultus* XIV, *C. punctatus* XIV).

GROWTH INCREMENTS

Because of the relatively low number of specimens observed, these results are not significant but they indicate the overall tendency.

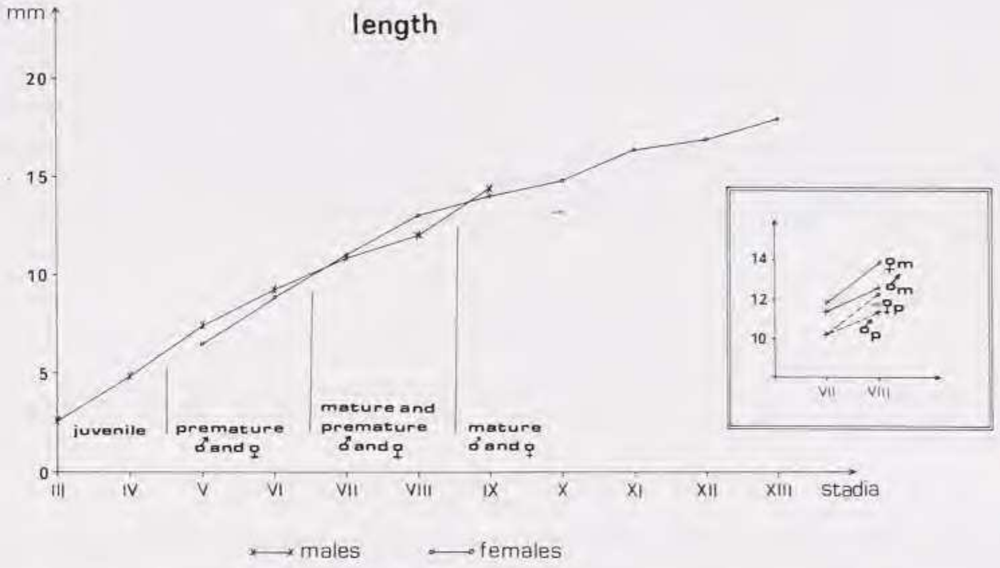

FIG. 3. — Mean increase of length in *C. latestriatus* (p = premature, m = mature individuals).

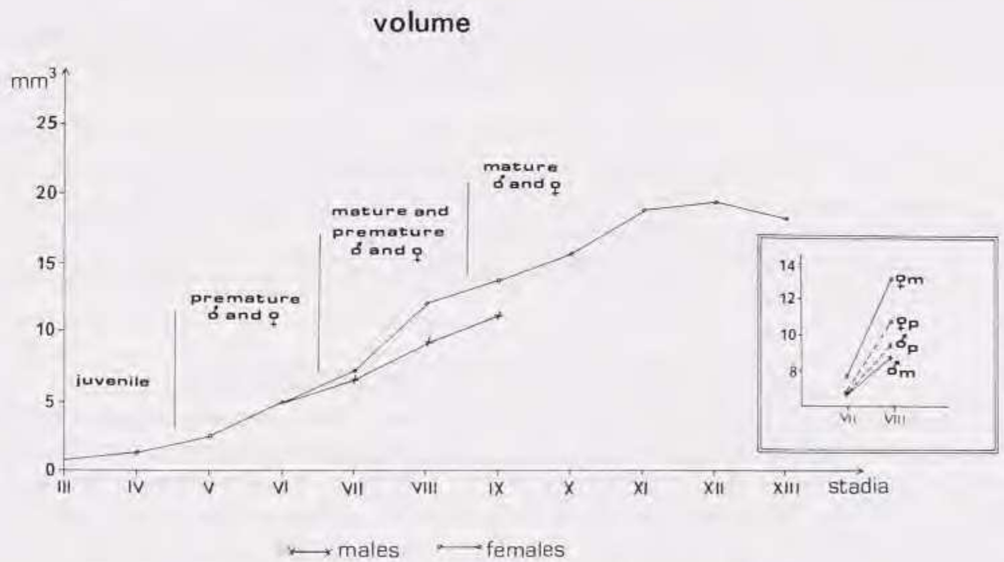

FIG. 4. — Mean increase of volume in *C. latestriatus*.

Each moult of *C. latestriatus* is correlated with a relatively constant increase of length (Fig. 3). The same is true for the volume except for the XIIIth stadium of females (Fig. 4). Judging from the biomass (Fig. 5), more or less identical results can be seen, with the exception of some flattened sections of the curves for gravid females according to the number of eggs. In contrast the numbers of newly formed rings decrease at each moult.

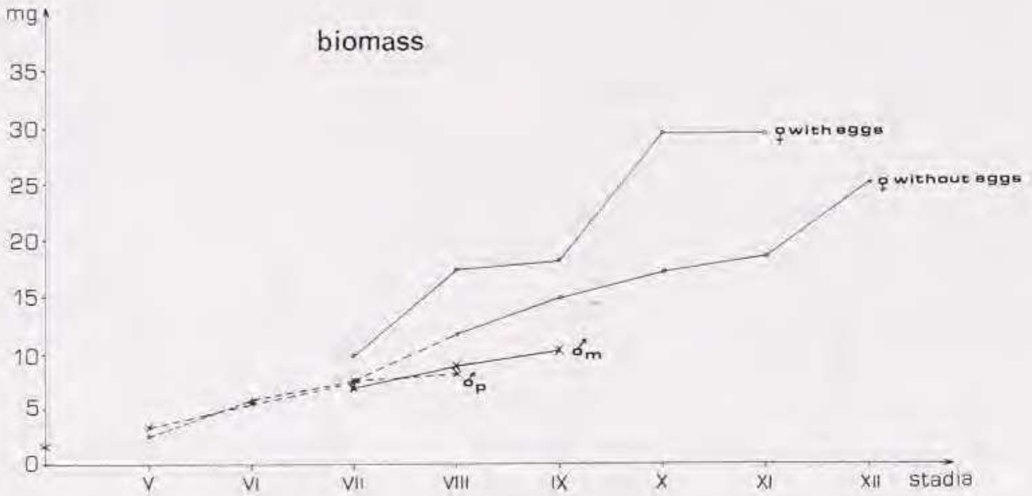

FIG. 5. — Mean increase of biomass of *C. latestriatus*.

ENGHOFF, DOHLE & BLOWER (1993) have suggested 4 hypotheses to explain the range of addition of rings. According to these, the addition can depend on:

1. the available energy ,
2. the randomness of splitting of the germinal field,
3. a combination of 1+2,
4. a predisposition to variable increments for whatever reason.

As to point 1, observations on *C. latestriatus* cannot be explained by different energy supply if we suppose that available energy is not continously decreasing from stadium IV to the end.

Furthermore the growth in biomass is not closely related to the numbers of added rings.

Regarding hypothesis 2 it should be considered that the first 3 stadia have an entirely constant increment, and after that there is a nearly constant decrease of addition from the Vth stage on. These events cannot be explained by randomness.

A predisposition of some kind may be assumed, although the cause has not yet been identified.

EGG LAYING AND EARLIEST DEVELOPMENT

BLOWER & GABBUTT (1964) did not find any eggs neither in the field nor in culture. They assume, that eggs are laid in small numbers and not aggregated together in a typical nest.

In this study one nest was found consisting of 6 eggs in a rearing vessel in the laboratory at the beginning of May. The pupoids "hatched" after two weeks and developed after 4 days into a typical stadium I with 3 pairs of legs. The duration of this stadium was 3 to 4 days. The following stadium II is the first free living and feeding one. All observed young specimens overwintered at stadium V.

SEXUAL DIMORPHISM AND BEGINNING OF MATURITY

The sexes of *C. latestriatus* can be distinguished first at stadium V. Premature males clearly show the absence of the leg pairs on the 7th body ring. Animals with appearance of females need a further moult to clarify the real sex.

In all investigations made in *C. latestriatus* both sexes reached maturity in stadium VII or rarely in VIII. In females the eggs, which can be seen through the body wall, indicate the maturity.

BLOWER & GABBUTT (1964) have investigated precisely the gonopod development of some species. They pointed out, that 2 to 3 gonopod stadia exist in *C. latestriatus*, which extend over 5 developmental stadia of the males. The primary gonopod stage always coincides with the fifth stage, the secondary and also the tertiary with the sixth. Mostly, maturity is reached in stadium VII, rarely the tertiary gonopod stage extends to stadium VIII or IX (1 male). Corresponding with their investigations only 20% premature males in stadium VIII were found here, but no premature specimens in stadium IX.

Females reached the highest stadium of XII in their natural habitat (Table 2) and stadium XIII in the laboratory (only ?). Males reach a maximum of stadium VIII (with the exception of one male in stadium IX). This suggests that males die mostly after one or certainly after two reproduction periods.

TABLE 2. — Moulting activity of *C. latestriatus*.

Month	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
juvenile + premature	2	1	2	12		12	3	2	2	-	-
mature	-	-	2	5	4	4	10	6	18	3	3
Total	2	1	4	17	4	16	13	8	20	3	3

The temporal distribution of the moults is shown in Table 2. Juveniles, premature and mature individuals are able to moult over the whole year, but with different maxima. Adults mostly moult in autumn, juveniles and prematures in spring and summer. This agrees with other characteristics of the species such as the high locomotory activity of adults in spring during the search for the partners. A moult is the peak of the physiological activity and can only take place after the end of a reproduction period. Young individuals can moult in spring too, because they do not reproduce.

AGE STRUCTURE AND LIFE CYCLE

The age structure of the population is strongly connected with the life cycle of *C. latestriatus*. The population consists of all stadia and age groups throughout the whole year with exception of the youngest stadia, which can only be found after the egg laying period.

As a consequence of the different speeds of the individual development, individuals of several generations can belong to the same stadium. This may firstly be observed in stadium VI with two overlapping generations. In stadium VIII the overlap can include 3 generations. This fact makes the interpretation of samples very difficult. This is the reason why a combination between field observations and results of laboratory rearings was necessary.

The egg laying takes place in spring. The young individuals develop, according to the results of all authors, into the stadia (III), mostly IV or V (and VI) in which they overwinter. Individuals of stadium VI may belong to the first generation or to the second if they started from overwintered stadium III. Provided that the maturity moult takes place in autumn

(VOIGTLÄNDER, 1987) it is concluded, that the first reproduction is possible at the 2nd or 3rd year of life. This short time for development is very uncommon for julids.

Males die after one or at least two reproduction periods. They live for a maximum of 3 or 4 years, as a rule only 2-3 years. Females have on average a higher expectation of life usually 3-4 years, with a maximum of 7-8 years.

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